



Research Article

Gradual change and mosaic pattern of macrofaunal assemblages along depth and sediment gradients in a tropical oceanic island

Jeffrey A. Sibaja-Cordero^{1,2}, Jesús S. Troncoso¹¹ Universidad de Vigo, Departamento de Ecología y Biología Animal, Facultad de Ciencias del Mar, Campus Lagoas Marcosende, Vigo, Spain² Universidad de Costa Rica, Centro de Investigación en Ciencias del Mar y Limnología (CIMAR) and Escuela de Biología, San Pedro, San José, Costa RicaCorresponding author: Jeffrey A. Sibaja-Cordero (jeffrey.sibaja@ucr.ac.cr)

Abstract

The ecology of macrofauna on the sandy bottom of oceanic islands in the tropics has rarely been studied. The present study was conducted at Isla del Coco, Costa Rica, a tropical oceanic island, to determine how the soft-bottom macrofauna assemblages vary along different levels of ocean exposure and their associated environmental conditions. The macrofauna was collected from five grabs at each of the 27 stations (between 3 and 75 m deep) in April 2010. The broad-scale pattern consists of a gradual increase in the complexity of assemblages (taxonomical or feeding guilds in the sediment) from the inner part to the outside of the bays. The leading determinant of this pattern was the interplay between ocean exposure and sediment variation with depth that produces habitat heterogeneity. The main taxa responsible for differences between ocean exposure zones were the polychaetes *Westheidesyllis heterocirrata* and *Magelona californica*, the filter-feeding bivalve *Gouldia californica*, and the predatory isopod *Eurydice caudata*. Coarse bottoms had more mobile predators and suspension feeders, whereas passive suspension feeders or subsurface deposit feeders dominated fine sands. The deeper stations were dominated by organisms feeding actively on particles from the water or on the sediment surface. Moreover, more feeding guilds were found in deeper waters. Additionally, at the small-scale view (grabs within each station), macrofauna composition evidences a mosaic pattern, mainly at the inner and middle of the bays, caused by biological or environmental disturbances.

Key words: gradients, natural disturbance, patchy distribution, small-scale pattern

Academic editor: Maria Lopez Selva

Received: 27 December 2023

Accepted: 22 April 2024

Published: 28 June 2024

ZooBank: <https://zoobank.org/8F268AAB-281E-443A-B928-02E1897DCF08>

Citation: Sibaja-Cordero JA, Troncoso JS (2024) Gradual change and mosaic pattern of macrofaunal assemblages along depth and sediment gradients in a tropical oceanic island. In: Lipińska M, Lopez-Selva MM, Sierra JM (Eds) Biodiversity research in Central America. Neotropical Biology and Conservation 19(2): 293–318. <https://doi.org/10.3897/neotropical.19.e117876>

Copyright: This is an open access article distributed under the terms of the CC0 Public Domain Dedication.

Introduction

Benthic communities can follow three possible pathways concerning environmental gradients: ecocline, ecotone, and mosaics (Johnson 1972; Atrill and Rundle 2002). In the ecocline, transitions between two systems are gradual due to changes in at least one environmental factor. The result is that species distributions may overlap (Johnson 1972; Gray 1974; Atrill and Rundle 2002). In an ecotone, the change is relatively rapid, producing a boundary between discrete (homogeneous) assemblages with environmental stability within them. However, the limits on ecotones can be dynamic (unstable) because of stress zones created

by abrupt environmental changes (Johnson 1972; Atrill and Rundle 2002). In this context, the assemblages are discrete units or part of a continuum of the whole community (Gray and Elliot 2009). The third community pathway, the mosaic, comprises fragments or sub-mixed communities (Atrill and Rundle 2002). Mosaics are usually the result of small local disturbances in the sediment at different times (Johnson 1972; Alongi 1989). In this way, a sample or a sample set has different possible successional stages, or a polyclimax (Gray and Elliot 2009).

Each species is present in a particular environment, possibly interacting with other species and with environmental factors (Mills 1969). The variety of interactions produces the previous pathways at different spatial scales in benthic communities (Azovsky et al. 2000; Smale 2008). The changes in the seabed provide variability in tropical benthic communities due to such factors as depth, calcium carbonate content, organic matter, sedimentation, grain type, marine currents, and the mixing of the water column (Alongi 1989; Aller and Stupakoff 1996; McArthur et al. 2010). Other factors also play a determining role, such as interspecific or intraspecific competition, predation, larval settlement, and bioturbation (Alongi 1989; 1990; Murray et al. 2002).

In the Neotropics, several factors can change the structure of benthic assemblages (Alongi 1990). For example, the macrofaunal composition varies mainly due to an increase in depth and variations in sediment characteristics (Maurer and Vargas 1984; Rostad and Hansen 2001); thereby, the number of assemblages in a location is correlated with the variety of bottom types present (Mair et al. 2009; Valencia et al. 2014). However, the benthos also decreases in biomass and complexity under hypoxic conditions (Nichols-Driscoll 1976; León-Morales and Vargas 1998), rainfall, freshwater inputs, and landslide influences (Maurer and Vargas 1984; Alongi 1990). Several of the above factors have also been shown to positively affect several meiofaunal groups (Guzmán et al. 1987; Alongi 1990). Other sources of variation in tropical benthic communities are seasonal changes in sediment composition and water characteristics (Lee 1978; Cortés et al. 2012).

The tropical benthic macrofaunal communities are often dominated by certain feeding guilds, which are correlated with the availability of their food source (Lee 1978) and limited by their adaptations to bottom characteristics (Muniz and Pires 1999). Predators and suspension feeders tend to dominate on sandy bottoms due to the increase in interstitial space and resuspension of particles, respectively. Subsurface deposit feeders dominate mainly in muddy sediments with high organic matter content (Muniz and Pires 1999). Finally, tropical and subtropical macrofauna assemblages can be influenced by mechanical disturbances such as fish trawling activity, fish bioturbation (Rostad and Hansen 2001; Cortés et al. 2012), or other kinds of macro-predators (Aarnio et al. 1991; Van Son and Thiel 2006), producing patchiness in their distribution.

The Tropical Eastern Pacific region contains the oceanic islands of Revillagigedo, Clipperton, Galapagos, and Isla del Coco. Previous studies on subtidal sedimentary fauna on these islands primarily focused on species lists. These islands had been poorly studied regarding community composition and their ecology in marine sediments (Villamar and Cruz 2007; Sibaja-Cordero et al. 2012a). At Isla del Coco, the polychaete assemblages were studied in a bathymetric transect (5–76 m), showing the change in the identity of the species at the 50 m depth, possibly caused by the thermocline (Sibaja-Cordero et al. 2012a). Moreover, other taxonomic groups, such as mollusks and crustaceans,

were not studied in their association with the environmental conditions on the oceanic islands of TEP. The macrofauna of Isla del Coco, studied in the present paper, has been taxonomically characterized by Sibaja-Cordero et al. (2016), and their analysis indicated an increase in the number of species and total density from the inner zones of the bays to the exposed coast. The study by Sibaja-Cordero et al. (2016) did not determine the response of macrofauna assemblages to spatial and environmental gradients present in tropical oceanic islands. Therefore, the present study fills this information gap and provides insight into the spatial dynamics of this type of marine system (Alongi, 1990).

The present study describes how macrofaunal taxa and feeding guilds' composition varies from poorly-structured to complex-structured assemblages along an ocean exposure gradient. The three possible patterns of change along this gradient would be P1: discrete with ecotones; P2: gradual ecoclines; or P3: in a mosaic pattern.

In this way, it is expected that a greater dissimilarity between assemblages at different ocean exposure levels indicates the presence of ecotones (P1). Conversely, less difference in these similarities suggests the presence of an ecocline (P2). Additionally, because the influence of the environmental gradients can be negligible at a few meters or centimeters of distance, uniformity in the assemblages on a small scale (within sampling stations) is expected. Greater variation in assemblages, either within ocean exposure levels or stations (grab samples), suggests the presence of mosaics (P3). Finally, the patterns found in the composition of taxa and feeding guilds in this study were explained by the association of biological data with environmental variables.

Methods

Study area

Isla del Coco, a national park in Costa Rica, has been a World Heritage Site since 1997. This oceanic island is isolated by 495 km from the mainland and other insular territories (Lizano 2001). The island has an area of 24 km² (Weston 1992; Lizano 2001; Sibaja-Cordero 2008). The ecosystems protected around the island include an area of 11629 km² of marine waters, and the island has four bays, several cliffs, reefs, and sandy bottoms. The seasonality of Isla del Coco is caused by the influence of the North Equatorial Countercurrent, which carries warm waters from the Western Pacific from April to December (Lizano 2008). The insular platform was described by Lizano (2001), and the distribution and characteristics of the rocky and sedimentary bottom were presented by Sibaja-Cordero et al. 2012b, 2014). The island's platform is 18 km long. It extends in a southwest to northeast direction with its edge at 180 m depth, beyond which it rapidly becomes deep (Lizano 2001; Cortés and Blum 2008).

Data collection

Isla del Coco was visited during the UCR-UNA-COCO-I expedition using the MV Argo from 19 to 29 April 2010 with the permission of Conservation Area Isla del Coco, National System of Conservation Areas of the Ministry of Environment and Energy, Costa Rica. There was no precise mapping of the

bottom types prior to the present survey. Sampling was conducted at 42 stations around the island, but only 27 had a sedimentary bottom. The stations were not equidistantly spaced (Fig. 1) due to the distribution of rocky bottoms and coral reefs, isolated rocky crops, or coral colonies (Sibaja-Cordero et al. 2012b, 2014). In the southern region, only one station was sampled due to adverse weather during the expedition, while other stations in this region corresponded to rocky substrates. The stations were categorized according to levels of ocean exposure based on their position in the bays (inner, middle, outside of bays, and exposed coast) (Fig. 1). The depth was recorded and corrected to the low tide level for all stations. Five samples were taken at each of the 27 stations with a van Veen grab (sampling area of 25×25 cm, with 0.31 m^2 sampled per station) to study the macrofauna. An additional sample was taken for sediment analysis. The total organic matter [TOM] was determined by weight loss determination, the CaCO_3 percentage was measured by the back titration method, and the granulometric analysis was carried out following the Folk and Ward method (Sibaja-Cordero et al. 2014). In the laboratory, macrofauna samples were sieved through a $500 \mu\text{m}$ mesh, and individuals were extracted from the remaining sediment under a stereomicroscope. The taxa were identified using guides for mollusks (Keen 1971; Coan and Valentich-Scott 2012), polychaetes (de León-González et al. 2009; Dean et al. 2012), sipunculans (Dean et al. 2010), crustaceans (Fischer et al. 1995), and other invertebrates (Carlton 2007; Wehrtmann and Cortés 2009). A complete list of the taxa found is presented in Sibaja-Cordero et al. (2016).

Statistical analysis

Ecocline or ecotone

The commands in R to carry out the statistical analysis and graphs for the present study are presented in Suppl. material 2, and the species/station abundance matrix is presented in Suppl. material 3.

To determine if the macrofaunal composition changes gradually (P1: ecotones) or abruptly (P2: ecocline), the Chord Normalized Expected Species Shared (CNESS), a Euclidean distance variation between stations (pooling the five grabs per station), was carried out in R using the 'ness' package (Gallagher 1999; Menot 2019). The distances range from 0 (no dissimilarity) to the square root of 2 (two stations share no common species) and do not need any additional transformation of the raw data (Gallagher 1999; Trueblood et al. 1994). Rare taxa, such as species with one individual in a single sample, can play a significant role in clustering patterns; thus, all taxa are included in the analysis. The package chose the appropriate value of m (random draw of individuals) to make the CNESS matrix sensitive to both rare and dominant taxa (Trueblood et al. 1994; Gallagher 1999; Menot 2019). It is an advantage of CNESS over other conventional indexes (Gallagher 1999; Legendre and Gallagher 2001; Zou and Axmacher 2020). The m value was selected among the values ranging from $m = 1$ to $m =$ the total minimum data (30 in this study). Triangular matrices were correlated with the matrices using $m = 1$ and $m =$ min total; the best Kendall's Tau correlation was shown by the CNESS matrix using $m = 9$ (0.72 with $m = 1$, and 0.70 with $m = 30$) (Trueblood et al. 1994; Zou and Axmacher 2020).

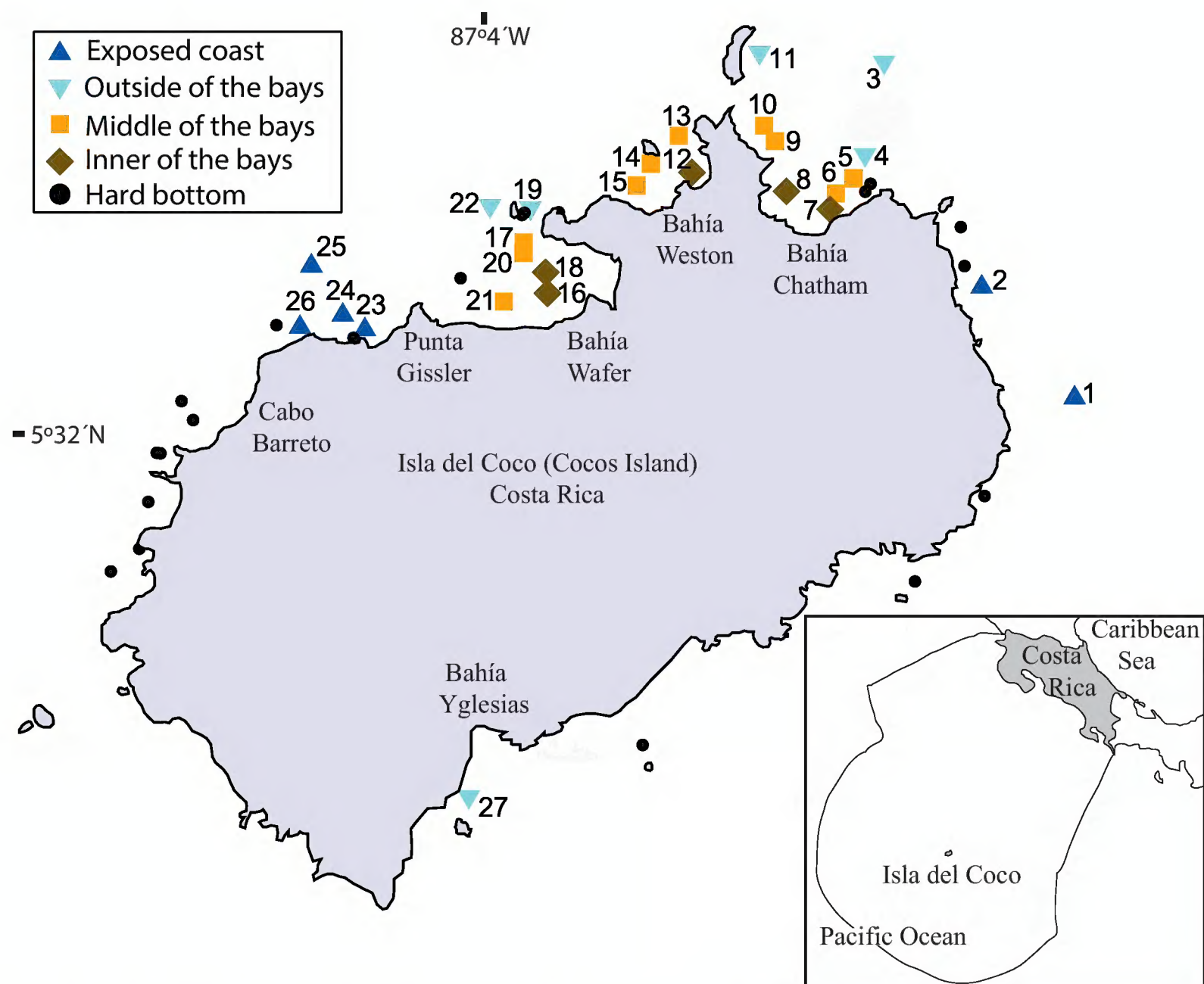


Figure 1. Stations (1–27) for grab sampling by levels of ocean exposure. Isla del Coco, Costa Rica. April 2010.

An analysis of similarities (ANOSIM) was performed to test the difference in composition of fauna between levels of ocean exposure (Fig. 1) using the CNESS ($m = 9$) with pairwise ANOSIMs as a posthoc test, using the “vegan” package in R and the software PAST (Clarke and Warwick 1994; Hammer et al. 2001; Oksanen 2015). The value of R indicates the amount of separation of the groups of stations (levels) (Clarke and Warwick 1994); if R is 1, it means no shared taxa between the levels, while a value close to zero indicates no difference between levels (Clarke and Warwick 1994). In this way, the amount of separation can be interpreted as the presence of an abrupt (P1) to a gradual change (P2) in the species composition between levels of ocean exposure. The R -value can be substantially less than zero, but this indicates incorrect labeling of the samples, or the presence of an important stratifying factor not evaluated (Clarke and Warwick 1994). A non-metric multidimensional scaling (nMDS) was plotted from the CNESS matrix ($m = 9$) to represent the similarity of the stations by levels of ocean exposure using “vegan” (Oksanen 2015).

Additionally, a similarity percentage (SIMPER) was used to determine the contribution of each taxon to the dissimilarity between levels of ocean exposure in cases of significant differences in the ANOSIM (Clarke and Warwick 1994). The SIMPER was performed in software PAST using a Euclidean distance of the abundance data matrix transformed to a hypergeometric probability (H' matrix) (Gallagher 1999). The elements in the H' matrix are the probability of sampling each taxon at each station with a random draw ($m = 9$). This matrix was normalized: the sum of squares of the elements in each row [station] is 1.

The matrix was also centered: each element minus the column [taxa] means. The Euclidean distance of the H' matrix is the same as that of the CNESS triangular matrix ($m = 9$) mentioned previously (Gallagher 1999; Legendre and Gallagher 2001; Zou and Axmacher 2020).

Presence of a mosaic pattern

The degree of internal variability (Beta diversity) can be interpreted as an indicator of a mosaic pattern (P3) in the benthic fauna caused by biological or environmental perturbation (Johnson 1970; Alongi 1989; Anderson et al. 2006). An index of multivariate dispersion (IMD) was carried out to measure the degree of internal variation, with the command `betadisper` in “vegan” (Oksanen 2015). This index was calculated for each station as the mean distance of each of the five grab samples from the centroid of the station. It was calculated based on the H' matrix, $m = 1$, in Suppl. material 5. The average IMD among levels of ocean exposure and stations was tested with an ANOVA test (Oksanen 2015).

Environmental association

The BIOENV analysis and Mantel test in “vegan” were used to relate the biological dissimilarity matrix (CNESS, $m = 9$) with environmental data (Suppl. material 4). Previously, sediment fractions were analyzed in a cluster analysis based on the Pearson correlation distance using the simple linkage method. To reduce the data matrix used in the subsequent analysis, this cluster identified the sediment fractions that are most highly correlated (Sibaja-Cordero et al. 2019). The cluster was used to make groups of sediment fractions that better discriminate between the stations. These new fractions, the parameters of the sediment's distribution (sorting, kurtosis, skewness, and mean grain size), TOM and CaCO_3 percentage, and depth were analyzed in a principal component analysis of correlation, using R to determine the highly positive correlated variables (Sibaja-Cordero et al. 2019). One variable representative of each group was selected, resulting in the following list: depth, TOM, CaCO_3 , skewness, gravel, medium, and fine sand fractions (Suppl. material 1). Before carrying out the BIOENV, these variables were transformed and checked to follow a normal distribution (Clarke and Warwick 1994).

BIOENV chooses the combination of variables that best explain the biological data using the harmonic Spearman correlation (rw) (Clarke and Warwick 1994). The best association from BIOENV between the environmental and biological matrix was graphed with a diastemogram using LOESS smoothing. This procedure made a nonparametric adjustment of the relationship between variables (Legendre and Gallagher 2001; Crawley 2007). If the LOESS line increases monotonically as sites get further apart in the gradient, it can represent an ecocline (Legendre and Gallagher 2001). The nMDS of CNESS $m = 9$ with the superimposed variables of the BIOENV analysis were plotted. Additionally, profiles of the species distribution of the Annelida, Arthropoda, Mollusca, Cnidaria, and other groups were plotted to visualize their correlation with each of these variables (Suppl. materials 7–10).

Additionally, a null matrix was constructed for the ocean exposure levels. This null matrix would have 0's in all within-level comparisons, indicating no

intralevel distance, and 1's in all of the among-level comparisons of ocean exposure as differences due to this factor (Rundle and Jackson 1996). This null matrix and the geographical distance between stations ("fossil" package of R) were related to the biological and environmental variables using a partial Mantel test to check for spatial autocorrelation in the "vegan" (Rundle and Jackson 1996; Sklenár and Jørgensen 1999; Vavrek 2011).

Feeding guild composition

The feeding guilds assigned were suspension feeder: active, passive, or mixed strategy; deposit feeder: surface, subsurface, or mixed strategy; predator: sessile or mobile; scavenger; and herbivore based on indirect reference to species or genus feeding guilds in the literature (McDonald et al. 2010; Jumars et al. 2015).

The matrix of abundance per taxon by station (Suppl. material 3), the matrix of feeding guilds by taxon (Suppl. material 6), the levels of ocean exposure, and the reduced matrix of environmental variables (see Environmental association section) were related using an RLQ ordination analysis (in the "Ade4" package in R) to obtain the feeding guilds by environmental variables relationship (Wesuls et al. 2012). The significance of ocean exposure levels and their contribution to total inertia was used as an indication of an abrupt (P1) pattern. The significant contribution of other environmental variables indicated a gradual change in feeding guild composition along these gradients (P2). The contribution of the feeding guilds to the total inertia was also calculated. Only the environmental variables associated with the RLQ axis were presented in the biplot (Wesuls et al. 2012).

Results

Ecocline or ecotone

Taxa composition presents a separation between zones (ANOSIM with an R-value = 0.26, $p = 0.003$). Exposed coast stations were similar in taxa composition to the outer bay stations ($R = -0.08$, $p = 0.741$). In contrast, the stations in the middle of the bays differed from the exposed coast stations ($R = 0.22$, $p = 0.044$) but not from the adjacent stations outside of the bays ($R = 0.14$, $p = 0.097$). Finally, stations at the inner area of the bays were more different in composition of macrofauna than the other zones (exposed coast: $R = 0.46$, $p = 0.014$; outside of the bays, $R = 0.49$, $p = 0.012$; and middle of the bays, $R = 0.45$, $p = 0.003$).

The change of taxa composition from the exposed coast and outside the bays, towards the middle and the inner regions of these bays, was represented from left to right of Dimension 1 on the nMDS (Fig. 2). Several stations outside of the bays and on the exposed coast were grouped together (Fig. 2). Within this group, the deeper stations 3, 22, and 25 show a high similarity in their fauna (Fig. 2). The stations from the middle of the bays were clustered into two groups of stations on the eastern side (5, 13, 17, and 20) and the western side of the bays (9, 10, 14, 15, and 21). Station 8 at the interior of Chatham Bay was separated from the rest of the stations in the inner regions of the bays (7, 12, 16, 18), which was the most dissimilar in faunal composition (Fig. 2).

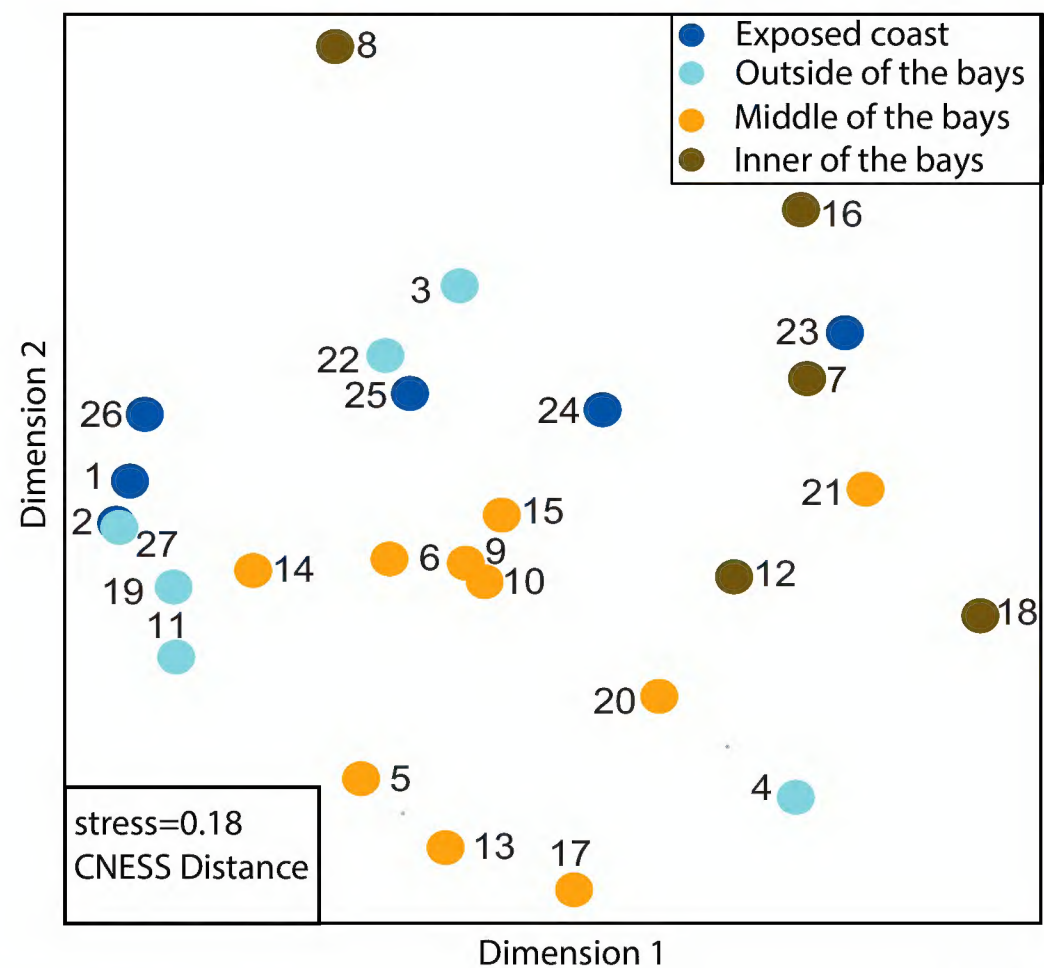


Figure 2. Benthic macrofaunal assemblages by ocean exposure levels. Isla del Coco. Multidimensional scaling (nMDS) shows the similarity (CNESS, $m = 9$) of macrofauna between stations by exposure to ocean influence. Stress = 0.18, non-metric fit = 0.97

The taxa contribution by levels to ocean influence was obtained using SIMPER analysis (Table 1). Twenty taxa contributed to 80% of the difference between levels of exposure. The taxa with higher abundances outside of the bays were the nematodes, with $p > 0.800$ (hypergeometric probability) of those that had been sampling at this level of ocean exposure, and the bivalve *Gouldia californica* (Table 1). The syllid *Westhedesyllis heterocirrata* and the pisionid *Pisone cf. galapagoensis*, were common at the exposed coast. The isopod *Eurydice caudata*, tended to have the highest abundances in the deeper stations (1 and 3) and exposed coast (station 26). The probability of sampling these species on the exposed coast was $p > 0.430$ (Table 1).

The species that characterized the middle of the bays were the tanaidacean *Cocotanais puravida*, the sipunculid *Aspidosiphon (Aspidosiphon) muelleri muelleri*, the polychaete *Prionospio (Prionospio) sp.*, and oligochaetes with probabilities between 0.249 and 0.450 (Table 1).

The following polychaete taxa occurred with a higher probability ($p > 0.400$) at stations in the inner of the bays: *Scoelepis (Scoelepis) squamata*, *Magelona californica*, and *Prionospio sp.* (Table 1). The second group of species that defined the inner zone of the bays with a probability between 0.400 and 0.250 were the polychaetes *Rhynchospio glutaea* and *Neanthes acuminata*, the sipunculid *Siphonosoma cumanaense*, and the crustaceans Thalassinidea (Table 1).

Presence of a mosaic pattern

The lower mean variability of multivariate dispersion was found in the exposed coast stations, and the higher mean value was found in the middle of the bays (Fig. 3, $F = 4.47$, d.f. = 3/23, $p = 0.013$). Several stations in the inner, middle, and outside of the bays had significantly higher internal variability of their

Table 1. Results of SIMPER analysis showing the first twenty taxa by their contribution (C%) in the average dissimilarity (A.D.) of CNESS (m=9) of the macrofauna between the levels of ocean exposure and their mean hypergeometric probability.

Taxon	Phylum	A.D.	C %	Cum %	Inner	Middle	Outside	Exposed
Adenophorea indet.	N	0.09342	7.893	7.893	0.407	0.669	0.804*	0.765
<i>Westheidesyllis heterocirrata</i> (Hartmann-Schröder, 1959)	A	0.09305	7.861	15.75	0.010	0.357	0.352	0.477*
<i>Magelona californica</i> Hartman, 1944	A	0.09019	7.62	23.37	0.675*	0.605	0.187	0.259
<i>Pisone</i> cf. <i>galapagoensis</i> Westheide, 1974	A	0.07736	6.536	29.91	0.022	0.290	0.279	0.437*
<i>Scolecipis</i> (<i>Scolecipis</i>) <i>squamata</i> (O. F. Muller, 1806)	A	0.07727	6.528	36.44	0.388*	0.041	0.003	0.334
<i>Prionospio</i> (<i>Prionospio</i>) sp.	A	0.07107	6.004	42.44	0.268	0.450*	0.297	0.280
<i>Eurydice caudata</i> Richardson, 1899	Cr	0.05222	4.412	46.85	0.000	0.135	0.110	0.403*
<i>Prionospio</i> sp.	A	0.04876	4.119	50.97	0.411*	0.333	0.255	0.234
Boloceroidea indet.	Cn	0.04351	3.676	54.65	0.327*	0.263	0.180	0.021
<i>Cocotanais puravida</i> Esquete, 2013	Cr	0.04128	3.487	58.14	0.031	0.268*	0.130	0.000
Thalassinidea indet.	Cr	0.03834	3.239	61.38	0.338*	0.063	0.000	0.000
<i>Neanthes acuminata</i> Ehlers, 1868	A	0.03804	3.214	64.59	0.342*	0.001	0.003	0.000
<i>Rhynchospio glutaea</i> (Ehlers, 1897)	A	0.02892	2.443	67.03	0.261*	0.000	0.000	0.000
<i>Gouldia californica</i> Dall, 1917	M	0.02876	2.43	69.46	0.000	0.077	0.232*	0.013
<i>Aspidosiphon</i> (<i>Aspidosiphon</i>) <i>muelleri muelleri</i> Diesing, 1851	S	0.02823	2.385	71.85	0.005	0.249*	0.144	0.030
Oligochaeta indet. B	A	0.02642	2.232	74.08	0.105	0.258*	0.127	0.123
Melitidae indet.	Cr	0.02328	1.966	76.05	0.060	0.014	0.147*	0.073
<i>Siphonosoma cumanense</i> (Keferstein, 1867)	S	0.02232	1.886	77.93	0.351*	0.053	0.016	0.088
<i>Aonides paucibranchiata</i> Southern, 1914	A	0.02228	1.883	79.81	0.000	0.020	0.138*	0.129

Cn = Cnidaria, Cr = Crustacea, N = Nematoda, M = Mollusca, A = Annelida, S = Sipuncula.
* Maximum hypergeometric probability for each taxon

samples (grabs) (over the mean multivariate dispersion) than the rest of the stations within their ocean exposure level ($F = 3.14$, d.f. = 26/108, $p < 0.001$, Fig. 3). It indicates a patchy distribution of the populations within these stations (mosaic pattern P3) at a small spatial scale (Fig. 3).

Environmental association

The cluster of the sediment fractions indicates that gravel (>2000 μm), coarse (<2000 to >710 μm), medium (<710 to >250 μm), and fine sand (<250 μm) were the sediment types that better describe the bottom environment (Suppl. material 1: fig. S1A). The PCA of environmental variables (Suppl. material 1: fig. S1B) showed that depth was positively correlated with the mean grain size and coarse sand, and the gravel sand was positively correlated with the sorting. In this way, the depth, gravel, TOM, CaCO_3 , skewness, and fine sand are representative variables of the environmental gradients (Suppl. material 1: fig. S1B) to take into account in their association with the assemblages.

The BIOENV analysis of these variables (after transformation, Shapiro-Wilk: $p > 0.05$ for each variable) selected the depth (m) and fine sand (%) as the main environmental gradients that together best explained the patterns found in the community assemblages (Spearman $r = 0.49$). The x-axis of the diastemogram

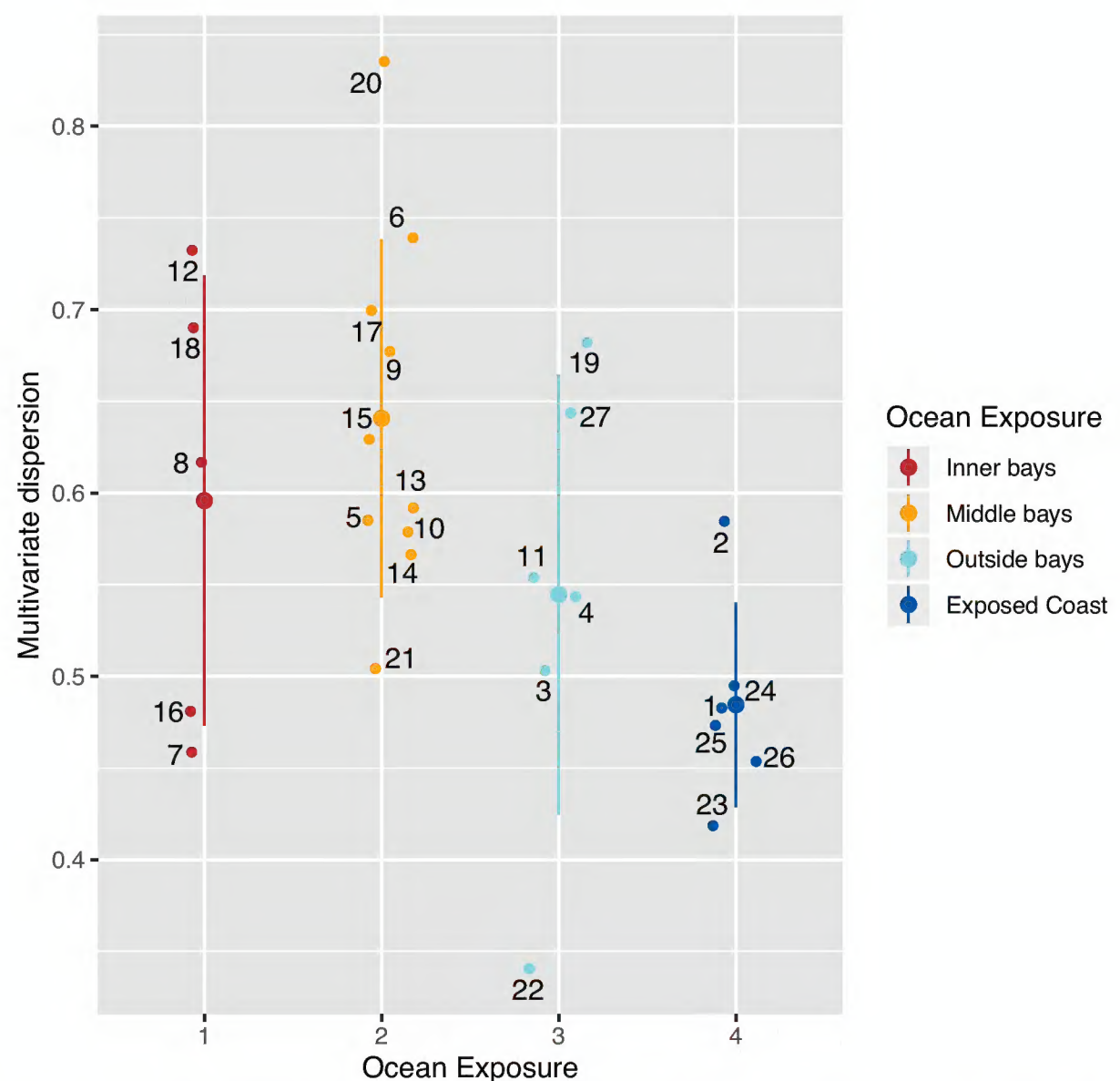


Figure 3. Multivariate dispersion of macrofaunal grab samples from each station (numbers 1–27) and their median value by ocean exposure levels. Isla del Coco, Costa Rica, April 2010.

(Fig. 4A) represents depth and fine sand. It shows that a greater environmental difference (euclidean distance) created a greater change in the macrofaunal composition. These variables for themselves were correlated in a lower degree with the CNESS dissimilarity matrix (Table 2).

The depth was related to the change in species identity in each taxonomic group. Several species are not present in shallow waters, but some species present in shallow waters have a wide bathymetric distribution (Suppl. material 8). The distribution of macrofauna shows a group of 55 of the 267 taxa present only at < 20 m depth, and 51 taxa were present only at > 50 m depth (Suppl. materials 7, 8). The remaining 155 species had a wider depth distribution but were absent in one or more stations. The Annelida presented 34 taxa only at < 50 m depth and 24 taxa only at > 50 m of their 100 species (Suppl. material 8). A total of 40 taxa of arthropods (Crustacea and Chelicerata) were found only at < 50 m and ten species only at > 50 m depth. Mollusks share a few species between depth ranges, with only three of the 40 taxa distributed along the depth gradient and nine only present at >50 m depth. Other groups, such as cnidarians, flatworms, and chordates, also showed a change in the identity of their taxa with depth (Suppl. materials 7, 8).

The percentage of fine sand was higher in the middle and inner bays and dropped in the more exposed stations (Fig. 4C). The high values of silt and clay promote the separation of stations 8 and 18 (inner bay) from other inner bay stations (Fig. 4C). On the other hand, at the outside of bays and exposed coasts, the depth increased (Fig. 4B), along with gravel and medium sand.

Table 2. BIOENV and Mantel correlations and probabilities for the environmental variables (after transformation) with the macrofauna similarity (CNESS) of sampling stations in Isla del Coco.

Correlation	Macrofauna con CNESS	
	R	p
All variables	0.38	<0.001
BIOENV 1° selection	0.49*	<0.001
Depth and Silt-Clay		
BIOENV 2° selection	0.47	<0.001
Depth, Silt-Clay, and TOM		
Depth (m)	0.31	0.001
TOM (%)	0.14	0.07
CO ₃ (%)	0.11	0.117
Gravel (%)	0.18	0.029
Medium sand (%)	0.31	0.003
Fine sand (%)	0.44	0.001
Skewness	0.01	0.443
Geographic distance between stations	−0.01	0.521
Ocean Exposure	0.19	0.003
Partial Mantel	0.49	0.001
CNESS with BIOENV, Controlled by Geographic distance between stations		
Partial Mantel	0.43	0.001
CNESS with BIOENV, Controlled by Ocean Exposure		

* The best combination of predictors.

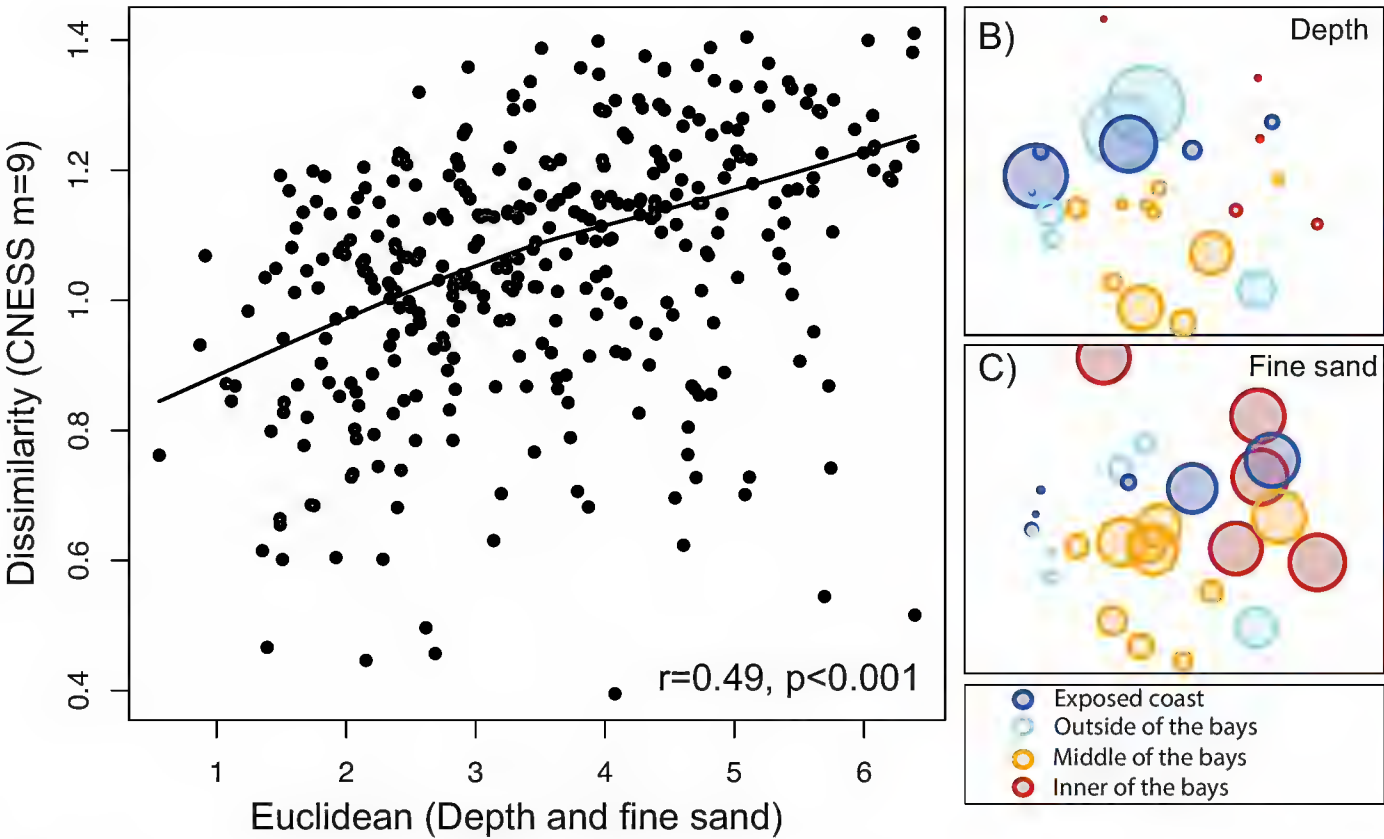


Figure 4. Association of macrofauna with environmental variables. Diastemogram (A) showed the association between the dissimilarity matrix of the macrofauna (CNESS m = 9) and the dissimilarity matrix of environmental variables based on BIOENV using the LOESS smoothing method. nMDS of stations based on their macrofauna includes overlapped circles representing (B) the depth (m) and (C) fine sand (%).

The BIOENV also found a second environmental variable group that includes TOM (%) as the third variable contributing to the patterns seen in the macrofauna (Table 3). In this way, TOM explained a few of the changes in the composition of fauna because they only had high values in the inner bays with more fine sediments. The assemblages in stations with higher values of fine sand (mainly silt-clay fractions) were less diverse and structured (Suppl. material 10). Four species (two annelids, one mollusk, and a Labridae fish) of the 267 were only found in sediments with $\geq 90\%$ fine sand. Another 13 species were only found in sediments with $\geq 60\%$ fine sand (one annelid, three mollusks, seven arthropods, a hydrozoan, and another Labridae fish). In sediments with $< 60\%$ fine sand, the number of species found was 161, but only 62 were present in sediments with $< 5\%$ fine sand. This loss of species towards the fine sediments was found in all the taxonomic groups (Suppl. materials 9,10).

The assemblages show a low association with the ocean exposure levels ($r = 0.19$, Mantel test) because the change is gradual and more related to the previously mentioned environmental gradients (depth-sediment); the ocean exposure gradient per se had a low contribution in explaining the change of the assemblages, as indicated by the partial Mantel correlation ($r = 0.46$ by depth and fine sand, controlled by the effect of ocean exposure) (Table 2). Some spatially neighboring stations have differences in depth and sediment that reduce their similarity (for example, the eastern and western sides in the middle of the bays). At the same time, stations at different bays showed similar assemblages when their environmental values and exposure to the ocean were similar. In this way, non-spatial autocorrelation was found to affect the composition of the assemblages (Table 2).

Feeding guild composition

Depth, granulometric, and TOM gradients present significant contributions ($>8\%$) to determining the pattern found with RLQ ordination (Table 3, Fig. 5). However, ocean exposure does contribute a little to explaining the pattern, with only the middle of the bays contributing 4.88% of the significant contribution. The change in the feeding guild of the assemblages was mainly gradual (P2) following the ecoclines imposed by depth, grain size, and TOM synergy.

Passive suspension feeders and deposit feeders contribute most to the patterns of separation between stations (Table 4), but suspension feeders (active or facultative) show the most association with the environmental gradients (Table 4).

The zones with fine sands (mainly inner bays) were dominated by passive suspension feeders (SFp) and species that can switch to deposit feeding (SFa-D). The subsurface deposit feeding guild (Dss) also contributed to this association between the feeding method and fine sediments (Fig. 5).

The surface or mixed strategy deposit feeders (Ds and Dm) were present in stations with higher TOM, and suspension feeder-predators (SFp-Ps), like anthozoans, were found in the middle of the bays.

Mobile predators (Pm) and scavengers (Sca) were most abundant with the increase in gravel and medium sand fractions, especially in stations outside the bays. Additionally, suspension feeders with mixed strategies to feed (SFm) were found in this type of bottom, but mainly on the exposed coast (Fig. 5).

Table 3. Percentage of contribution to the inertia of each environmental variable in the RLQ ordination. The Pearson correlation test of each environmental variable and the test of association for ocean exposure level with the RLQ axis are shown.

RLQ	Environmental variables				
Variable	% Contribution	Axis 1		Axis 2	
		Test	p	Test	p
Exposed coast	6.22	0.21	0.470	0.37	0.973
Outside of the bays	3.88	0.33	0.938	0.20	0.439
Middle of the bays	4.88	0.31	0.310	0.21	0.029**
Inner of the bays	8.79	0.10	0.143	0.18	0.591
Depth	17.04	0.06	0.669	-0.29	0.002**
Fine sand	14.09	0.28	0.009**	0.08	0.469
TOM	12.18	0.21	0.070*	-0.16	0.152
Medium sand	9.95	-0.23	0.038**	-0.05	0.645
Gravel	8.60	-0.19	0.098*	-0.08	0.493
CaCO ₃	7.74	0.07	0.570	-0.18	0.091*
Skewness	6.63	0.12	0.313	0.08	0.470

Significance levels: * $p \leq 0.10$, ** $p \leq 0.05$.

Table 4. Percentage of contribution to the inertia of each feeding guild group in the RLQ ordination. The test of association for feeding guilds to the RLQ axis is shown. Significance levels: * $p \leq 0.10$, ** $p \leq 0.05$.

Feeding guilds	% Contribution	Axis 1		Axis 2	
		Test	p	Test	p
Suspension feeder, passive (SFp)	17.10	0.02	0.961	0.01	0.283
Surface deposit feeder (Ds)	13.41	0.17	0.234	0.20	0.518
Subsurface deposit feeder (Dss)	11.11	0.09	0.943	0.06	0.429
Mobile Predator (Pm)	10.68	0.15	0.121	0.19	0.708
Suspension feeder, active – Deposit feeder (SFa-D)	10.64	0.00	0.598	0.00	0.687
Suspension feeder, passive – Sessile predator (SFp-Ps)	9.82	0.03	0.127	0.04	0.149
Suspension feeder, mixed strategy (SFm)	9.47	0.00	0.088*	0.01	0.653
Deposit feeder – Mobile Predator (D.Pm)	5.87	0.41	0.655	0.37	0.192
Deposit feeder, mixed mode (Dm)	4.56	0.00	0.397	0.00	0.240
Suspension feeder, active (SFa)	4.09	0.02	0.018**	0.01	0.001**
Mobile Predator – Scavenger (Pm-Sca)	2.83	0.00	0.110	0.01	0.302
Herbivore (H)	0.21	0.00	0.973	0.00	0.992
Suspension feeder, passive – Surface deposit feeder (SFp-Ds)	0.11	0.00	0.168	0.00	0.088*
Scavenger (Sca)	0.11	0.00	0.439	0.00	0.590

Finally, active suspension feeders (SFa) and passive forms that can act as sessile predators (SFp-Ds) were dominant in the deeper zones and outside the bays. The deeper zones of coarse carbonate sediments had the most types of feeding guilds on the island (Fig. 5).

Discussion

Ecocline or ecotone

Johnson (1972) indicated that if the environment is a gradient, communities will be gradually distributed. If the environmental change is abrupt, the result will be discrete communities. The results of the ordinations and ANOSIM for 267 taxa of Isla del Coco indicate a gradual change (P2) in the composition from the inner of the bays to more exposed stations. In Hong Kong, Shin and

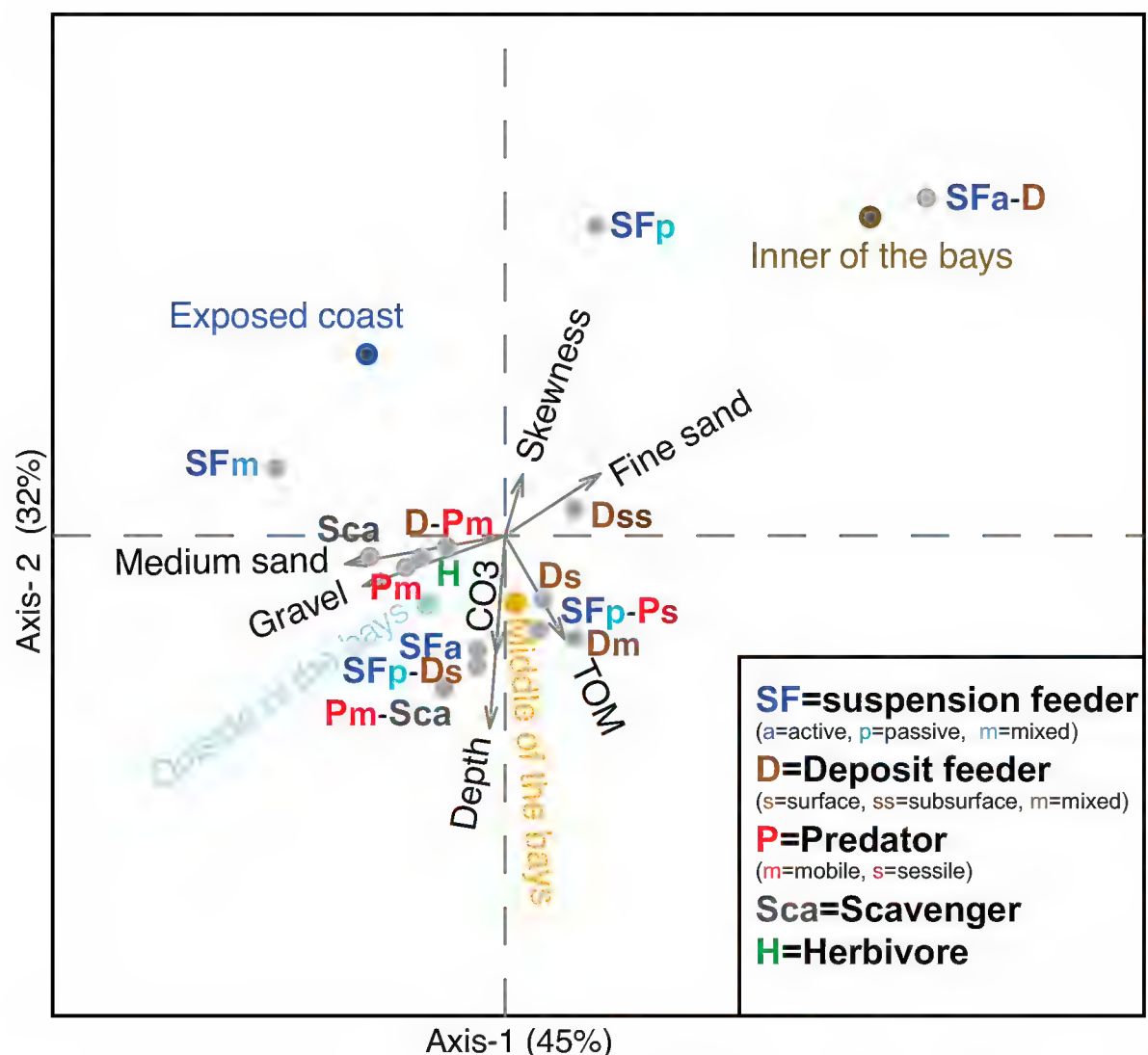


Figure 5. RLQ ordination showing the association of feeding guilds with environmental variables. Isla del Coco, Costa Rica, April 2010.

Thompson (1982) found five groups of stations at a cut-off level with 24% similarity in the benthic faunal composition. Perhaps due to the lower similarity level of macrofauna between the groups, they found environmental differences in depth, grain size, and salinity. A similar result was found in Isla del Coco, with a maximum of 49% separation between levels of ocean exposure due to the inherent variation between stations at each level. However, the environmental factors of the depth and composition of the sediments explain the groups better than the ocean exposure level. Still, these gradients change in most of the results of other studies in this direction (Alongi 1990; McArthur et al. 2010).

Johnson (1972) indicated that taxa assemblages are determined by environmental factors, producing a list of recurring taxa but in variable combinations. In this sense, as occurs in Isla del Coco, some species can be excluded from the assemblage at specific values of a factor, and other species could be banned at harsher environmental conditions imposed by another factor. It is partially concordant with the nestedness pattern mentioned by Checon et al. (2018) as a possible way in which biological communities are structured. Moreover, the synergy of factors acting as filters (Menegotto et al. 2019) results in the variability of the assemblages of each exposure ocean level. It promotes a gradual change in the macrofauna composition, as occurs in the present study.

Presence of a mosaic pattern

The inherent variation within the stations at each level of ocean exposure in Isla del Coco can be attributable to small-scale processes such as biological interactions on a short time scale (Alongi 1989), and it should be viewed as patchiness resulting in a mosaic distribution (Johnson 1972; Alongi 1989;

Menegotto et al. 2019). The sediment is also subject to continuous disturbances (bioturbation by dwellings and macropredators, river input, or currents). The resulting community is a collection of survivors of previous disturbances at different stages of succession (Johnson 1972).

The influence of macro-predators was proposed as a cause of the increase in the variability of the benthic macrofauna near the rocky reefs than far from them, in the south of Australia (34 °S) (Barros et al. 2001). During dives at Isla del Coco, demersal fish such as flounder and rays were seen foraging on the sediment, creating holes (~30 cm), which resulted in small-scale disturbances (pers. obs.), similar to the observations in the study of Australia (Barros et al. 2001). In Isla del Coco, the highest variability was found in the middle of the bay, at sites with better development of rocky and coral reefs. Alongi (1990) mentioned the existence of a positive correlation between benthic biomass and fish-diverse communities. Additionally, at least a quarter of tropical demersal fish are benthic predators, and 38% are hunters of fish and benthic fauna (Alongi 1990). In Isla del Coco, the fish assemblages associated with these reefs that can be foraging on the sandy bottom contribute to the patchiness of the macrofauna.

Moreover, other stations at the inner of the bays varied slightly between their samples by low abundances ($n < 100$ individuals) or considerably between their samples (patchiness). The influence of abrupt river discharges could wash away the assemblages in the inner bays, or the bottom could be layered with fine-soil particles challenging to colonize (Snelgrove 1999). The stations on the exposed coast were internally homogeneous in their faunal composition. Most of these stations have coarse and mixed sediments (Sibaja-Cordero et al. 2014), and species such as *W. heterocirrata*, *P. cf. galapagoensis*, and the isopod *E. caudata* had abundant populations. The heterogeneity of sediments in these stations can allow dense patches of these species due to habitat availability and the refuge of predators (Alongi 1989; Gray and Elliot 2009).

Stations outside of the bays, such as stations 4 and 11 at Chatham, have many individuals but lower variation among samples, possibly due to the topography of the sediment. The presence of valleys and dunes on the seabed can influence the macrofauna and the settlement of larvae (McArthur et al. 2010; Anderson et al. 2013). Weston Bay had many valleys and dunes, while in Manuelita, the bottom was more homogeneous (pers. obs. during dives), explaining why station 11 had a more homogeneous fauna than Weston Bay.

Finally, stations on the eastern side of the middle of the bays were more similar to more exposed stations than those on the western side of the bays. Storm currents could explain this degree of separation as the influence of storm swells can modify the seabed (Anderson et al. 2013), in this case differing on the two sides of the bays. In this way, abiotic factors shape communities on a large scale. In contrast, biotic factors shape it on a small scale (Snelgrove 1999). Still, the presence of ephemeral biotic or abiotic perturbations can modify the structure of an assemblage punctually (Alongi 1989).

Environmental association

As discussed before, the macrofaunal assemblages were influenced by environmental factors. Isla del Coco responds to the synergy between depth and sediment gradients (BIOENV test), producing the gradual change found in species composition.

The depth gradient on this tropical oceanic island results in various microhabitats that different taxa combinations can inhabit. Several species present in deeper waters were not distributed to shallow waters. On the other hand, some species were found all along the depth gradient. In general, species loss was gradual, but two depth points (25 and 50 m) show a significant decrease in richness. The organisms in the rocky walls of the island also changed drastically at depths greater than 50 m (Cortés and Blum 2008), producing some degree of vertical zonation in rocky subtidal benthos. Previous data concerned with polychaetes collected in Bahía Chatham found that density and richness were low at 50 m depth and composition of assemblage change by turnover or gain of species at > 50 m (Sibaja-Cordero et al. 2012a), similar to the present study.

These previous studies pointed out the location of a thermocline, which seemed to limit the distribution of macrofauna. The surface waters of the island ranged in temperature from 27 to 29.5 °C (Acuña-González et al. 2008). Below the thermocline (at 50 m), the water was at 13 °C (Cortés and Blum 2008). The thermocline could vary in depth from year to year depending on the El Niño and La Niña stages of ENSO and variations between localities. These differences in the water column could affect settlement processes, recruitment, and survival of some groups but not others based on the parameters of the water column or seabed (McArthur et al. 2010). The ecological processes affecting tropical benthic animals in this context require further investigation. For example, in the subtidal rocky cliffs of the Galapagos, invertebrates vary in their recruitment and survival depending on the physicochemical properties of the water column (Witman and Smith 2003). Therefore, recruits exposed to the oscillation of the thermocline in Isla del Coco could be affected.

Additionally, several types of sedimentary bottom occur at Isla del Coco in the shallow waters (Sibaja-Cordero et al. 2012b), and this may explain the gradual loss of species present at shallow depth, similar to the effect of depth and fine sediment gradients in the tropical islands of Las Perlas, Panama (Mair et al. 2009). The results of the present study are consistent with other previous studies in the tropics, which found that the composition of benthic fauna was linked to sediment type (Shin and Thompson 1982; Maurer and Vargas 1984; Guzmán et al. 1987; Jayaraj et al. 2008). The depth gradient of the Isla del Coco seabed results in microhabitats that differ in grain size and can be populated by different combinations of taxa. The tendency is that with the increase in depth, the sediment becomes coarser and more heterogeneous and has the most complex assemblages (Maurer and Vargas 1984; Mair et al. 2009).

The degree of exposure to ocean influence could result in the instability of coarse sediments on the outside of the bays and deeper waters. In such a case, the abrupt slope sites can only be occupied by taxa with adaptations to stabilize or bury faster in the sediments (Murray et al. 2002). Sedimentary environments exposed to constant perturbations have less structured assemblages (Aller and Stupakoff 1996). In the case of Isla del Coco, the higher compaction of fine carbonate sand and fine sediments from river inputs with <250 µm mean grain size reduced the possibility of macroinfauna burying in them (Mills 1969). The fine sediment layer over the bottom represents a barrier for many species to move or use their respiratory or feeding apparatus efficiently, and it seems to be the cause of species loss in this gradient (Menegotto et al. 2019).

In benthic environments, habitat heterogeneity increases the complexity of the assemblages (Gray 1974; Probert and Wilson 1984), and at intermediate levels of disturbance, it maintains pioneer and late succession species (Connell 1978; Nichols 1979). In heterogeneous sediments, species that differ in their selection of grain size may coexist at small spatial scales (Johnson 1972), as in the exposed stations 1, 2, 14, and 19 of Isla del Coco. Another source of heterogeneity in these sediments was the presence of small rhodoliths, or fragments, buried in these four stations. These structures create microhabitats in the bottom sediment that increase the number of taxa (adding epifauna and cryptic taxa) with the increase in habitat heterogeneity (McArthur et al. 2010). The rhodoliths at Isla del Coco showed 1.8% of the total abundance and 41 benthic taxa, 13 of which were exclusive to this microhabitat.

The depth and sediment gradients explain the increase in taxa richness and compositional change towards the exposed coast of the island. On the other hand, the fine sediments of the inner portions of the bays presented few taxa and low abundances, producing less structured assemblages due to the negative influence of river inputs (Maurer and Vargas 1984; Guzmán et al. 1987).

Feeding guild composition

Feeding guild composition changes gradually (P2) following the gradient imposed by depth, TOM, and sedimentary features. Shallow waters with fine sediments, especially of the inner of the bays, were dominated by passive suspension feeders [SFp], such as *S. (S.) squamata*, and active suspension feeders that can act as surface deposit feeders [SFa-D], such as mud crabs (Thalassinidea). These feeding guilds coexist and dominate the shallow waters (< 50 m) in other tropical benthic systems (Posey 1986; Alongi 1989; Murray et al. 2002). Furthermore, these feeding guilds can survive disturbances occurring in the inner parts of the bays, such as freshwater input or the washing of sediment beds. For example, mud crabs can excavate the fine sediment layer deposited by the rivers, and spionid polychaetes act as small opportunistics (Posey 1986; Alongi 1989; Aller and Stupakoff 1996). These represent taxa able to use the particles that sink to the bottom (Alongi 1989; Murray et al. 2002; Menegotto et al. 2019), similar to the significant abundances of opportunistic spionids (surface deposit feeders) that dominated the Amazon shelf (Aller and Stupakoff 1996).

Additionally, subsurface deposit feeders [Dss], such as the oligochaetes, occur mainly in fine sediments in the inner and middle of Chatham Bay. Other deposit feeder groups had a higher abundance of fine or stable sediments with high TOM values. The stable sediments at deeper stations and in the middle of bays had the presence of cnidarians of the infraorder Boloceroidaria. These cnidarians are sessile predators that can also feed on suspension material (Anderson et al. 2013; Esquete et al. 2013).

The amount of suspended material in coarse sediment was low, and few suspension feeders were found. These bottoms were dominated by mobile forms that could be predators or deposit feeders. Most of the mobile organisms were polychaetes, which can use the tridimensional space of this coarse sediment to forage, detect, and capture prey (McDonald et al. 2010; Anderson et al. 2013). These species of suspension feeders that can use the low amount

of organic matter in carbonate sand as facultative surface deposit feeders are expected for this type of sediment (Alongi 1989). A similar pattern was found in India (Jayaraj et al. 2008), with zones dominated by predators and deposit feeders and others with deposit and suspension feeders depending on the food availability and granulometric variation.

More active suspension feeders (e.g., the bivalve *G. californica*) were found on the outside where the depth increased, and most of them fed on coral reef detritus. In fact, suspension feeders are more efficient at obtaining food than deposit feeders when they occur in carbonate sediments (Alongi 1989; Murray et al. 2002).

Conclusions

The macrofauna assemblages of Isla del Coco followed a gradual change in composition from the inner of the bays to the deeper and exposed zones (P2). This change was also observed in the taxonomical identity and the composition of feeding guilds. Assemblages were less structured in the inner areas of the bays, while more exposed and deeper stations showcased assemblages with higher abundances and greater diversity in feeding guild composition. The leading cause of this change was the synergy of depth with sediment composition. The depth gradient on Isla del Coco results in a variety of microhabitats that different taxa or feeding group combinations can inhabit. Predators dominated the deeper, coarser, and more unstable sediments, while passive suspension feeders inhabited shallow and stable sediments. Zones with high TOM exhibited more deposit feeders. Biological and environmental disturbance factors contribute to the variation in species composition (mosaics), mainly at small spatial scales (P3).

Acknowledgements

We thank Jorge Cortés for the organization of the UCR-A-COCO-I expedition to Isla del Coco. We also thank the rangers of Parque Nacional Isla del Coco, the staff of Centro de Investigaciones en Ciencias del Mar y Limnología (CIMAR), the Universidad de Costa Rica (UCR), and the Undersea Hunter crew of the MV Argo. Thanks to all the people who helped with their collaboration and reviewed the drafts of the manuscript.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

No funding was reported.

Author contributions

Conceptualization: JAAS, JST. Investigation: JAAS, JST. Supervision: JST. Writing - original draft: JAAS. Writing - review and editing: JST.

Author ORCIDs

Jeffrey A. Sibaja-Cordero  <https://orcid.org/0000-0001-5323-356X>

Jesús S. Troncoso  <https://orcid.org/0000-0002-7305-6879>

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

References

- Aarnio K, Sandberg E, Bonsdorff E (1991) Benthic predation on shallow-water macro- and meiofauna in the Baltic Sea: An experimental comparison between *Pomatoschistus minutus* (Pisces) and *Saduria entomon* (Crustacea). *Annales Zoologici Fennici* 28(1): 41–48.
- Acuña-González J, García-Céspedes J, Gómez-Ramírez E, Vargas-Zamora JA, Cortés J (2008) Parámetros físico-químicos en aguas costeras de la Isla del Coco, Costa Rica (2001–2007). *Revista de Biología Tropical* 56(S2): 49–56.
- Aller JY, Stupakoff I (1996) The distribution and seasonal characteristics of benthic communities on the Amazon shelf as indicators of physical processes. *Continental Shelf Research* 16(516): 717–751. [https://doi.org/10.1016/0278-4343\(96\)88778-4](https://doi.org/10.1016/0278-4343(96)88778-4)
- Alongi DM (1989) Ecology of tropical soft-bottom benthos: A review with emphasis on emerging concepts. *Revista de Biología Tropical* 37: 85–100.
- Alongi DM (1990) The ecology of tropical soft-bottom benthic ecosystems. *Oceanography and Marine Biology - an Annual Review* 28: 381–496.
- Anderson MJ, Ellingsen KE, McArdle BH (2006) Multivariate dispersion as a measure of beta diversity. *Ecology Letters* 9(6): 683–693. <https://doi.org/10.1111/j.1461-0248.2006.00926.x>
- Anderson TJ, McArthur MA, Syms C, Nichol S, Brooke B (2013) Infaunal biodiversity and ecological function on a remote oceanic island: The role of biogeography and bio-physical surrogates. *Estuarine, Coastal and Shelf Science* 117: 227–237. <https://doi.org/10.1016/j.ecss.2012.11.013>
- Atrill MJ, Rundle SD (2002) Ecotone or ecocline: Ecological boundaries in estuaries. *Estuarine, Coastal and Shelf Science* 55(6): 929–936. <https://doi.org/10.1006/ecss.2002.1036>
- Azovsky AI, Chertoproud MV, Kucheruk NV, Rybnikov PV, Sapozhnikov FV (2000) Fractal properties of spatial distribution of intertidal benthic communities. *Marine Biology* 136(3): 581–590. <https://doi.org/10.1007/s002270050718>
- Barros F, Underwood AJ, Lindegarth M (2001) The Influence of Rocky Reefs on Structure of Benthic Macrofauna in Nearby Soft-sediments. *Estuarine, Coastal and Shelf Science* 52(2): 191–199. <https://doi.org/10.1006/ecss.2000.0734>
- Carlton JT (Ed.) (2007) *The Light and Smith Manual: Intertidal Invertebrates from Central California to Oregon*, 4th edn. University of California Press, California, 1001 pp. <https://doi.org/10.1525/9780520930438>
- Checon HH, Corte GN, Shah Esmaeili YML, Amaral ACZ (2018) Nestedness patterns and the role of morphodynamics and spatial distance on sandy beach fauna: Ecological hypotheses and conservation strategies. *Scientific Reports* 8(1): 3759. <https://doi.org/10.1038/s41598-018-22158-3>
- Clarke KR, Warwick RM (1994) *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*. Bourne, Bournemouth, 128 pp.

- Coan EV, Valentich-Scott P (2012) Bivalve Seashells of Tropical West America. Marine Bivalve Mollusks from Baja California to Northern Perú, Monographs, Number 6, Studies in biodiversity 4. Santa Barbara Museum of Natural History, California, 1258 pp.
- Connell JH (1978) Diversity in Tropical Rain Forests and Coral Reefs. *Science* 199(4335): 1302–1310. <https://doi.org/10.1126/science.199.4335.1302>
- Cortés J, Blum S (2008) Life to 450 m depth at Isla del Coco, Costa Rica. *Revista de Biología Tropical* 56(S2): 189–206.
- Cortés FA, Solano OD, Ruíz-López JA (2012) Variación espacio-temporal de la fauna macrobentónica asociada a fondos blandos y su relación con factores ambientales en el Parque Nacional Natural Gorgona, Pacífico colombiano. *Boletín de Investigaciones Marinas y Costeras* 41: 323–353.
- Crawley MJ (2007) *The R Book*. John Wiley, New York, 942 pp.
- de León-González JA, Bastida-Zavala JR, Carrera-Parra LF, García-Garza ME, Peña-Rivera A, Salazar-Vallejo SI, Solís-Weiss V (Eds.) (2009) *Poliquetos (Annelida: Polychaeta) de México y América Tropical*. Universidad Autónoma de Nuevo León, Monterrey, 737 pp.
- Dean HK, Sibaja-Cordero JA, Cortés J, Vargas R, Kawauchi GY (2010) Sipunculids and Echiurans of Isla del Coco (Cocos Island), Costa Rica. *Zootaxa* 2557(1): 60–68. <https://doi.org/10.11646/zootaxa.2557.1.6>
- Dean HK, Sibaja-Cordero JA, Cortés J (2012) Polychaetes (Annelida: Polychaeta) of Cocos Island National Park, Pacific Costa Rica. *Pacific Science* 66(3): 347–386. <https://doi.org/10.2984/66.3.8>
- Esquete P, Sibaja-Cordero JA, Troncoso JS (2013) A new genus and species of Leptocheliidae (Crustacea: Peracarida: Tanaidacea) from Isla del Coco (Costa Rica). *Zootaxa* 3741(2): 228–242. <https://doi.org/10.11646/zootaxa.3741.2.2>
- Fischer W, Krupp F, Schneider W, Sommer C, Carpenter KE, Niem VH (Eds.) (1995) *Pacífico centro oriental; Guía FAO para la identificación de especies para los fines de la pesca Pacífico Centro-Oriental, Vol I, Plantas e Invertebrados*. FAO, Roma, 664 pp.
- Gallagher ED (1999) COMPAH documentation User's Guide and application. <http://www.es.umb.edu/edgwebp.htm>
- Gray JS (1974) Animal-sediment relationships. *Oceanography and Marine Biology - an Annual Review* 12: 223–261.
- Gray JS, Elliot M (2009) *Ecology of Marine Sediments, from Science to Management*, 2nd edn. Oxford University Press, New York, 255 pp. <https://doi.org/10.1093/oso/9780198569015.003.0005>
- Guzmán HM, Obando V, Cortés J (1987) Meiofauna associated with a Pacific coral reef in Costa Rica. *Coral Reefs* 6: 107–112. <https://doi.org/10.1007/BF00301379>
- Hammer Ø, Harper DAT, Ryan PD (2001) Past, Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica* 4: 1–9.
- Jayaraj KA, Sheeba P, Jacob J, Revichandran C, Arun PK, Praseeda KS, Nisha PA, Rashied KA (2008) Response of infaunal macrobenthos to the sediment granulometry in a tropical continental marginsouthwest coast of India. *Estuarine, Coastal and Shelf Science* 77(4): 743–754. <https://doi.org/10.1016/j.ecss.2007.11.016>
- Johnson RG (1970) Variations in Diversity within Benthic Marine Communities. *American Naturalist* 104(937): 285–300. <https://doi.org/10.1086/282662>
- Johnson RG (1972) Conceptual models of benthic marine communities. In: Schopf TJM (Ed) *Models in Paleobiology*. Freeman Cooper, California, 148–159
- Jumars PA, Dorgan KM, Lindsay SM (2015) Diet of Worms Emended: An Update of Polychaete Feeding Guilds. *Annual Review of Marine Science* 7(1): 497–520. <https://doi.org/10.1146/annurev-marine-010814-020007>

- Keen AM (1971) *Sea Shells of Tropical West America Marine Mollusks from Baja California to Peru*, 2nd edn. Stanford University Press, California, 1064 pp.
- Lee HII (1978) Seasonality, predation and opportunism in high diversity softbottom communities in the Gulf of Panama. Doctoral dissertation, University of North Carolina
- Legendre P, Gallagher ED (2001) Ecologically meaningful transformations for ordinations of species data. *Oecologia* 129(2): 271–280. <https://doi.org/10.1007/s004420100716>
- León-Morales R, Vargas JA (1998) Macroinfauna of a tropical fjord-like embayment, Golfo Dulce, Costa Rica. *Revista de Biología Tropical* 46(S6): 81–90.
- Lizano OG (2001) Batimetría de la plataforma insular alrededor de la Isla del Coco, Costa Rica. *Revista de Biología Tropical* 49(S2): 163–170.
- Lizano OG (2008) Dinámica de aguas alrededor de la Isla del Coco, Costa Rica. *Revista de Biología Tropical* 56(S2): 31–48.
- Mair JM, Cunningham SL, Sibaja-Cordero JA, Guzman HM, Arroyo MF, Merino D, Vargas R (2009) Mapping benthic faunal communities in the shallow and deep sediments of Las Perlas Archipelago, Pacific Panama. *Marine Pollution Bulletin* 58(3): 375–383. <https://doi.org/10.1016/j.marpolbul.2008.10.015>
- Maurer D, Vargas JA (1984) Diversity of softbottom benthos in a tropical estuary, Gulf of Nicoya, Costa Rica. *Marine Biology* 81(1): 97–106. <https://doi.org/10.1007/BF00397631>
- McArthur MA, Brooke BP, Przeslawski R, Ryan DA, Lucieer VL, Nichol S, McCallum AW, Mellin C, Creswell ID, Radke LC (2010) On the use of abiotic surrogates to describe marine benthic biodiversity. *Estuarine, Coastal and Shelf Science* 88(1): 21–32. <https://doi.org/10.1016/j.ecss.2010.03.003>
- McDonald TA, Burd BJ, Macdonald VI, van Roodselaar A (2010) Taxonomic and feeding guild classification for the marine benthic macroinvertebrates of the Strait of Georgia, British Columbia. Canadian Technical Report of Fisheries and Aquatic Sciences 2874: i–iv, 1–63.
- Menegotto A, Dambros CS, Netto SA (2019) The scale-dependent effect of environmental filters on species turnover and nestedness in an estuarine benthic community. *Ecology* 100(7): e02721. <https://doi.org/10.1002/ecy.2721>
- Menot L (2019) ncss: Hypergeometric standardization and probabilistic measures of similarity for community ecology. R package version 0.1.0. Zenodo. <https://doi.org/10.5281/zenodo.3254750>
- Mills EL (1969) The community concept in marine zoology, with comments on continuity and instability in some marine communities: A review. *Journal of the Fisheries Research Board of Canada* 26(6): 1415–1428. <https://doi.org/10.1139/f69-132>
- Muniz P, Pires AMS (1999) Trophic structure of polychaetes in the Sao Sebastiao Channel (southeastern Brazil). *Marine Biology* 134(3): 517–528. <https://doi.org/10.1007/s002270050567>
- Murray JMH, Meadows A, Meadows PS (2002) Biogeomorphological implications of microscale interactions between sediment geotechnics and marine benthos: A review. *Geomorphology* 47(1): 15–30. [https://doi.org/10.1016/S0169-555X\(02\)00138-1](https://doi.org/10.1016/S0169-555X(02)00138-1)
- Nichols FH (1979) Natural and anthropogenic influences on benthic community structure in San Francisco bay. In: Conornos TJ (Ed.) *San Francisco Bay: the urbanized estuary*. American Association for the Advancement of Science, California, 1–40
- Nichols-Driscoll J (1976) Benthic invertebrates communities in Golfo Dulce, Costa Rica, an anoxic basin. *Revista de Biología Tropical* 24: 281–297.
- Oksanen J (2015) Multivariate Analysis of Ecological Communities in R: vegan tutorial. <http://www.R-project.org>

- Posey MH (1986) Changes in a benthic community associated with dense beds of a burrowing deposit feeder, *Callianassa californiensis*. Marine Ecology Progress Series 31: 15–22. <https://doi.org/10.3354/meps031015>
- Probert P, Wilson J (1984) Continental Shelf Benthos off Otago Peninsula, New Zealand. Estuarine, Coastal and Shelf Science 19(3): 373–391. [https://doi.org/10.1016/0272-7714\(84\)90032-5](https://doi.org/10.1016/0272-7714(84)90032-5)
- Rostad T, Hansen KL (2001) The effects of trawling on the benthic fauna of the Gulf of Nicoya, Costa Rica. Revista de Biología Tropical 49(S2): 91–95.
- Rundle HD, Jackson DA (1996) Spatial and temporal variation in littoral-zone fish communities: A new statistical approach. Canadian Journal of Fisheries and Aquatic Sciences 53(10): 2167–2176. <https://doi.org/10.1139/f96-183>
- Shin PKS, Thompson GB (1982) Spatial Distribution of the Infaunal Benthos of Hong Kong. Marine Ecology Progress Series 10: 37–47. <https://doi.org/10.3354/meps010037>
- Sibaja-Cordero JA (2008) Vertical zonation in the rocky intertidal at Cocos Island (Isla del Coco), Costa Rica: A comparison with other tropical locations. Revista de Biología Tropical 56(S2): 171–187.
- Sibaja-Cordero JA, Cortés J, Dean HK (2012a) Depth diversity profile of polychaetes worms in Bahía Chatham, Isla del Coco National Park, Pacific of Costa Rica. Revista de Biología Tropical 60(S3): 293–301.
- Sibaja-Cordero JA, Troncoso JS, Benavides-Varela C, Cortés J (2012b) Distribution of shallow water soft and hard bottom seabeds in the Isla del Coco National Park, Pacific Costa Rica. Revista de Biología Tropical 60(S3): 53–66. <https://doi.org/10.15517/rbt.v60i3.28313>
- Sibaja-Cordero JA, Troncoso JS, Gómez-Ramírez E (2014) Recent surface marine sediments of Cocos Island in Costa Rica. International Journal of Sediment Research 29(1): 59–72. [https://doi.org/10.1016/S1001-6279\(14\)60022-6](https://doi.org/10.1016/S1001-6279(14)60022-6)
- Sibaja-Cordero JA, Troncoso JS, Cortés J, Moreira J, Benavides-Varela C (2016) Biodiversity and density of subtidal benthos of an oceanic tropical island (a comparison within the Pacific Ocean). Journal of Sea Research 115: 47–58. <https://doi.org/10.1016/j.seares.2016.07.004>
- Sibaja-Cordero JA, Camacho-García YE, Azofeifa-Solano JC, Alvado-Arranz B (2019) Ecological patterns of macrofauna in sandy beaches of Costa Rica: A Pacific-Caribbean comparison. Estuarine, Coastal and Shelf Science 223: 94–104. <https://doi.org/10.1016/j.ecss.2019.04.032>
- Sklenár P, Jørgensen PM (1999) Distribution patterns of páramo plants in Ecuador. Journal of Biogeography 26(4): 681–691. <https://doi.org/10.1046/j.1365-2699.1999.00324.x>
- Smale DA (2008) Continuous benthic community change along a depth gradient in Antarctic shallows: Evidence of patchiness but not zonation. Polar Biology 31(2): 189–198. <https://doi.org/10.1007/s00300-007-0346-3>
- Snelgrove PVR (1999) Getting to the Bottom of Marine Biodiversity: Sedimentary Habitats: Ocean bottoms are the most widespread habitat on Earth and support high biodiversity and key ecosystem services. Bioscience 49(2): 129–138. <https://doi.org/10.2307/1313538>
- Trueblood DD, Gallagher ED, Gould DM (1994) Three stages of seasonal succession on the Savin Hill Cove mudflat, Boston Harbor. Limnology and Oceanography 39(6): 1440–1454. <https://doi.org/10.4319/lo.1994.39.6.1440>
- Valencia B, Herrera L, Giraldo A (2014) Estructura de la comunidad y distribución vertical de la macrofauna de fondos blandos en isla Gorgona, Pacífico Colombiano. Revista de Biología Tropical 62(S1): 169–188. <https://doi.org/10.15517/rbt.v62i0.16274>

- Van Son TC, Thiel M (2006) Multiple predator effects in an intertidal food web. *Journal of Animal Ecology* 75(1): 25–32. <https://doi.org/10.1111/j.1365-2656.2005.01019.x>
- Vavrek MJ (2011) fossil: Palaeoecological and palaeogeographical analysis tools. *Palaeontologia Electronica* 14: 1–16.
- Villamar F, Cruz M (2007) Macrofauna bentónica en la zona intermareal y submareal en Caleta Aeolian, Isla Baltra (Galápagos, Ecuador). *Acta Oceanográfica del Pacífico* 14: 139–145.
- Wehrtmann IS, Cortés J (Eds.) (2009) *Marine Biodiversity of Costa Rica, Central America, Monographiae Biologicae* 86. Springer, San José, 538 pp. <https://doi.org/10.1007/978-1-4020-8278-8>
- Weston JC (1992) *La Isla del Coco/Cocos Island*. Trejos Hermanos Sucesores SA, San José
- Wesuls D, Oldeland J, Dray S (2012) Disentangling plant trait responses to livestock grazing from spatio-temporal variation: The partial RLQ approach. *Journal of Vegetation Science* 23(1): 98–113. <https://doi.org/10.1111/j.1654-1103.2011.01342.x>
- Witman JD, Smith F (2003) Rapid community change at a tropical upwelling site in the Galapagos, Marine Reserve. *Biodiversity and Conservation* 12(1): 25–45. <https://doi.org/10.1023/A:1021200831770>
- Zou Y, Axmacher JC (2020) The Chord-Normalized Expected Species Shared (CNESS)-distance represents a superior measure of species turnover patterns. *Methods in Ecology and Evolution* 11(2): 273–280. <https://doi.org/10.1111/2041-210X.13333>

Supplementary material 1

Cluster analysis

Authors: Jeffrey A. Sibaja-Cordero, Jesús S. Troncoso

Data type: eps

Explanation note: **fig. S1**. Cluster Analysis (A) of the sediment fractions (μm) and Principal Component Analysis (B) for correlations between environmental variables, Isla del Coco, Costa Rica. *The fraction of 250 μm was added to the group of medium sand for PCA.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/neotropical.19.e117876.suppl1>

Supplementary material 2

Command of R to carry out the analysis of data and figures of the macrofauna of Isla del Coco, Costa Rica

Authors: Jeffrey A. Sibaja-Cordero, Jesús S. Troncoso

Data type: R

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/neotropical.19.e117876.suppl2>

Supplementary material 3

Biological data of macrofauna in sediments of Isla del Coco, Costa Rica

Authors: Jeffrey A. Sibaja-Cordero, Jesús S. Troncoso

Data type: csv

Explanation note: The values are abundances of each of the 297 species, total abundance, and the number of species per station.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/neotropical.19.e117876.suppl3>

Supplementary material 4

Environmental data of benthic habitat of Isla del Coco, Costa Rica

Authors: Jeffrey A. Sibaja-Cordero, Jesús S. Troncoso

Data type: csv

Explanation note: The columns are longitude, latitude, depth in meters, % of total organic matter (TOM), % of carbonates (CaCO₃), % of each granulometric fractions (4000 to <63 µm), and parameters of the sediment distribution (sorting, skewness, kurtosis, and sort).

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/neotropical.19.e117876.suppl4>

Supplementary material 5

Standardized and normalized matrix of hypergeometric probabilities

Authors: Jeffrey A. Sibaja-Cordero, Jesús S. Troncoso

Data type: csv

Explanation note: Standardized and normalized matrix of hypergeometric probabilities (H' matrix with a draw of m = 1) of the macrofauna species by each sample of each station in sediments of Isla del Coco, Costa Rica.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/neotropical.19.e117876.suppl5>

Supplementary material 6

Feeding guilds by species of the macrofauna in sediments of Isla del Coco, Costa Rica

Authors: Jeffrey A. Sibaja-Cordero, Jesús S. Troncoso

Data type: csv

Explanation note: Codes are presented in Fig. 5 and Table 4.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/neotropical.19.e117876.suppl6>

Supplementary material 7

Species matrix sorting by depth at the bottom of Isla del Coco, Costa Rica

Authors: Jeffrey A. Sibaja-Cordero, Jesús S. Troncoso

Data type: csv

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/neotropical.19.e117876.suppl7>

Supplementary material 8

Depth profile for distribution of species by taxonomical group. Isla del Coco, Costa Rica

Authors: Jeffrey A. Sibaja-Cordero, Jesús S. Troncoso

Data type: eps

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/neotropical.19.e117876.suppl8>

Supplementary material 9

Species matrix sorting by fine sand percentage in the sediments of Isla del Coco, Costa Rica

Authors: Jeffrey A. Sibaja-Cordero, Jesús S. Troncoso

Data type: csv

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/neotropical.19.e117876.suppl9>

Supplementary material 10

Sedimentary profile (fine sand <250 µm) for distribution of species by taxonomical group. Isla del Coco, Costa Rica

Authors: Jeffrey A. Sibaja-Cordero, Jesús S. Troncoso

Data type: eps

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/neotropical.19.e117876.suppl10>